Jl S. Afr. Bot. 41 (2): 67–85 (1975)

STUDIES IN THE BULBOUS LILIACEAE IN SOUTH AFRICA: 5. SEED SURFACE CHARACTERS AND GENERIC GROUPINGS

J. P. Jessop
(*Schonland Botanical Laboratory, Rhodes University*)*

Abstract

Scanning electron microscope studies were made on the surface of the seeds of 49 specimens of 25 genera of South African Liliaceae. Five groups of genera of bulbous Liliaceae are recognised on the basis of seed surface characters.

It is suggested that three tribes should be recognised in the South African bulbous Liliaceae—the Scilleae, Massonieae and Bowieae. These are defined and the genera in each are listed.

Uittreksel

STUDIES VAN DIE BOLDRAENDE LILIACEAE IN SUID-AFRIKA: 5. KENMERKE VAN DIE SAADOPPERVLAK EN GENERIESE GROEPERINGS

Skandeer-elektronmikroskoop opnames van die saadoppervlak van 49 eksemplare van 25 genera Suid-Afrikaanse Liliaceae is gemaak. Vyf groepe genera van boldraende Liliaceae word erken op die basis van die saadoppervlakte kenmerke.

Dit word voorgestel dat drie tribusse boldraende Liliaceae in Suid-Afrika erken behoort te word—Scillae, Massonieae en Bowieae. Hierdie word defineer en die genera in elk gemeld.

Introduction

The South African bulbous Liliaceae genera have been placed in various tribes of the Liliaceae by different authors. It is generally agreed that the majority belong to a single tribe. Krause (1930) called the major group Scilloideae. *Schizobasis*, *Bowiea* and *Eriospermum* were included in a separate tribe—the Eriosperminae.

Hutchinson (1959) recognised the Scilleae and two other tribes—the Massonieae with two genera (*Massonia and Daubenya*) and the Bowieae with three genera (*Schizobasis*, *Bowiea* and *Eriospermum*).

Other authors have commented on the grouping of the bulbous genera, for example Phillips (1951) linked *Massonia* with *Polyxena*, *Neobakeria*, *Whiteheadia*, *Neopatersonia*, *Androsiphon* and *Amphisiphon* on the basis of their connate stamens, but no attempt has been made at revising tribal groupings.

---

* Present address: State Herbarium, Botanic Garden, Adelaide, S. Australia.

Accepted for publication 3rd January, 1975.

Generic concepts in the Scilleae still require attention. Jessop (1970 & 1972) has proposed a few generic changes, but there are several genera which may require redefinition—for example *Massonia* and *Drimia*. The genera at present recognised (excluding certain species belonging to the Aloineae) are:– *Schizobasis, Bowiea, Urginea, Rhadamanthus, Thuranthos, Drimia, Litanthus, Massonia, Daubenya, Androsiphon, Amphisiphon, Neobakeria, Polyxena, Hyacinthus, Veltheimia, Eucomis, Whiteheadia, Lachenalia, Ledebouria, Scilla, Drimiopsis, Neopatersonia, Galtonia, Pseudogaltonia, Ornithogalum, Elsiea, Albuca* and *Dipcadi.*

In an attempt to find a meaningful grouping of these genera, certain approaches have been tried, including the use of scanning electron microscope photographs of seed surfaces.

The assistance of Mr. R. H. M. Cross (Officer-in-charge of the Electron Microscopy Unit, Rhodes University) is gratefully acknowledged.

MATERIALS AND METHODS

The seed of 49 plants belonging to 43 species in 25 genera of Liliaceae were examined. Most of the material used was taken from herbarium specimens, but some fresh material was used. No differences in the seeds appeared to result from the use of dried material.

A thin layer of gold palladium alloy was evaporated onto the surface of the samples. The material was examined under a J.E.O.L. JSM U3 scanning electron microscope and in all cases photographs were taken.

OBSERVATIONS

The following brief descriptions are based on the photographs. Because of the limited material examined it is not considered justified to draw up more detailed descriptions.

Bulbine

B. frutescens (Ex hort., Rhodes University)

The concave, more or less isodiametric, cells with several papillae are not similar to those in any other material examined. Cells measure 160–240 μm diameter (Fig. 1A). This plant was included for comparison but is not bulbous.

Schizobasis

S. intricata (Klaasvoogds, Robertson (3319D), *Esterhuysen 22711*, BOL).

Sub-rectangular ridges probably represent cell margins, but their irregular arrangement suggests that they may be wrinkling, perhaps as a result of drying.

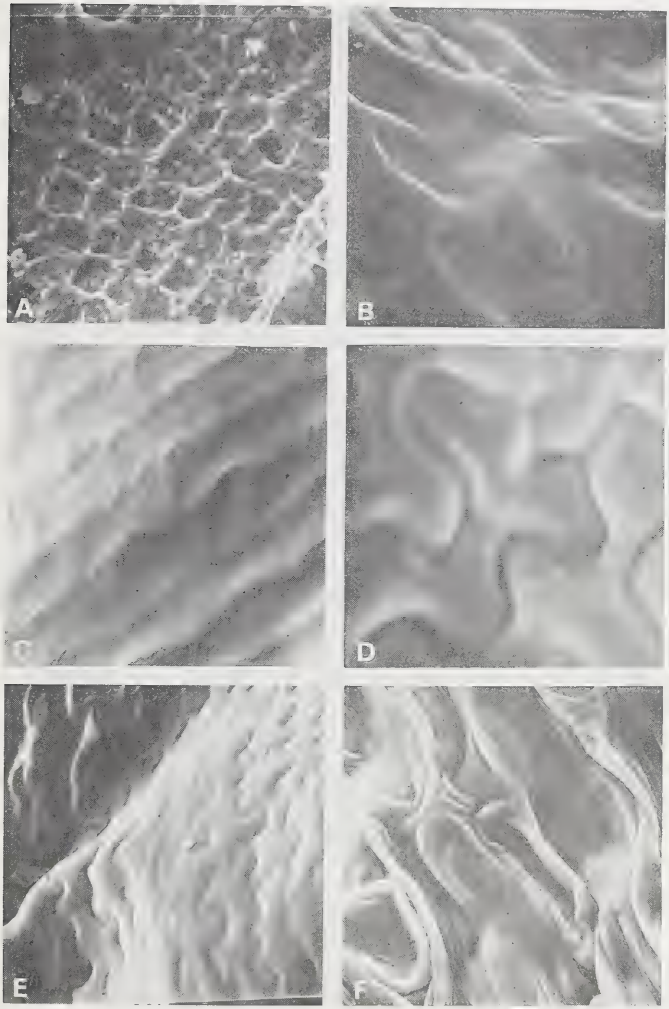

FIG. 1.
Scanning electron microscope photographs of Liliaceae seed surfaces. A. *Bulbine frutescens* (Ex hort., Rhodes University) x 300. B. *Schizobasis intricata* (*Esterhuysen* 22711) x 700. C. *Bowiea volubilis* (*Galpin s.n.*) x 200. D. *Albuca patersonii*. (*Martin s.n.*) x 700. E. *Galtonia princeps* (*Strey* 4516) x 200. F. *Drimia anomala* (*Esterhuysen* 18343) x 700.

There is some similarity with several species of *Drimia* and *Urginea*. 'Cells' concave with smooth surfaces (Fig. 1B).

Bowiea

B. volubilis (Byrne, Richmond, Natal (2930C), *Galpin s.n.*, BOL).

Rectangular convex cells with slightly undulate margins and a smooth surface are characteristic, but it is somewhat intermediate in form between *Urginea modesta* and *U. marginata*. It is also similar to *Galtonia princeps*. Cells measure 120–130 × 40–50 μm (Fig. 1C).

Albuca

A. canadensis (Huguenot College, Wellington, without collector, sub RUH *4473*, RUH).

Cells with smooth surface and undulate margins, 130–180 × 20–30 μm.

A. patersonii (Without locality, *Martin s.n.*, sub RUH *9548*, RUH).

Cells with smooth surface and more deeply undulate margins than in *A. canadensis*, c. 90–120 × c. 30 μm (Fig. 1D).

These two species are very similar to one another. The cell outline is similar to that of some species of *Urginea* and/or *Ornithogalum* but in those genera there are conspicuously raised areas in the seed surface which are absent in *Albuca*. There is a strong similarity with *Neopatersonia uitenhagensis*, which has pits however, and with *Galtonia princeps*, which has more rectangularly shaped cells.

Galtonia

G. princeps (Port Edward 3130A), *Strey 4516*, PRE).

Cells with smooth surface and undulate margins, c. 120–150 × c. 30 μm. The sub-rectangular cells are more deeply undulate than, but similar to, those of *Bowiea volubilis* (Fig. 1E).

Drimia

D. anomala (Uniondale, near Joubertina (3323D), *Esterhuysen 18343*, PRE).

Cells with contorted surface, minutely rough (the protuberances less than 1 μm diameter), 5- or 6-angled, 40–60 × 20–30 μm (Fig. 1F).

D. media (Great Drakenstein (3418B), *Esterhuysen 21348*, BOL).

Cells with more or less smooth surface, more or less rectangular, 80–200 × 40–50 μm (Fig. 2A).

Because of the probably very close relationship, *Drimia* is discussed at the end of the description of *Urginea*.

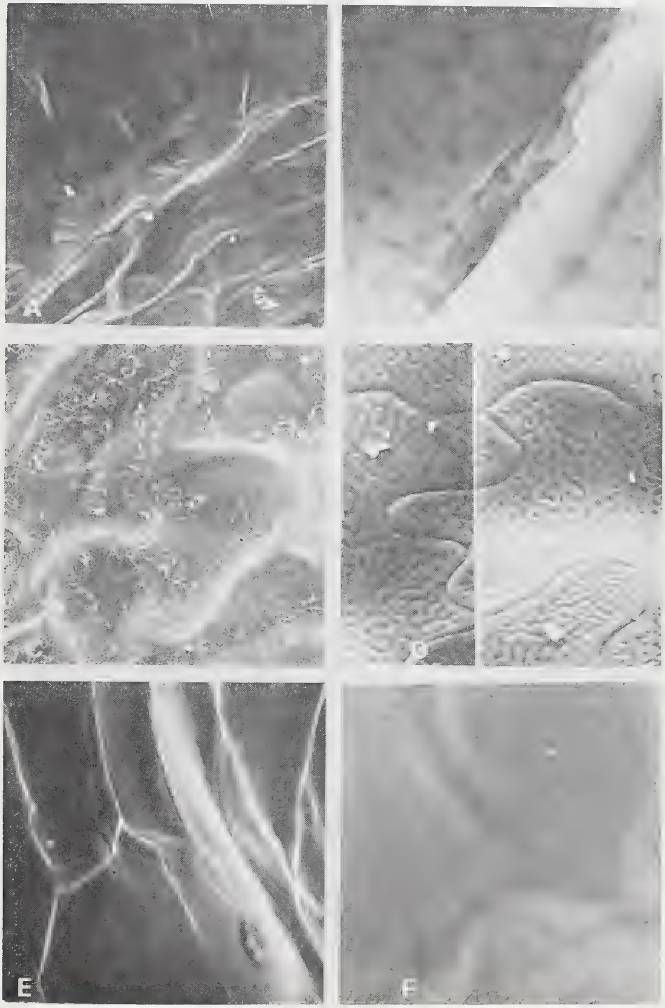

FIG. 2.
Scanning electron miscroscope photographs of Liliaceae seed surfaces. A. *Drimia media* (*Esterhuysen* 21348) x 200. *B. Urginea delagoensis* (*Buitendag* 118) x 2000. C. *Urginea basutica* (*Strey* 3128) x 200. D. *Urginea fragrans* (*Godfrey* VH-1254) x 700. E. *Urginea pusilla* (*Marloth* 857) x 700. F. *Urginea sanguinea* (*Marloth* 7686)x 700.

Urginea

U. delagoensis (Nelspruit (253OB), *Buitendag 118*, PRE).

Cells with pitted surface (the pits up to 1–1,3 μm diameter), otherwise smooth, rectangular, 300–400 × 40–60 μm (Fig. 2B).

U. basutica (Willow Glen, Pretoria (2528C), *Strey 3128*, PRE).

Cells with numerous curled threads and ribbons and pits (the pits c. 1–2 μm diameter), irregular in outline, convex, 80–230 × 70–120 μm (Fig. 2C). The threads and ribbons are removed by boiling briefly in water and are likely to consist of wax. They are, however, not soluble in Xylol at 20 °C.

U. fragrans (7 miles S. of Klaver (3118D), *Godfrey VH-1254*, PRE).

Cells with the surface covered by a dense reticulation of minute ridges (the ridges 1–1,5 μm thick), concave, the margins undulate and indicated by distinct grooves, 230–300 × 30–50 μm (Fig. 2D).

U. pusilla (Bultfontein, Kimberley (2824D), *Marloth 857*, PRE).

Cells with smooth surface, irregular in outline, 110–240 × 40–70 μm (Fig. 2E).

U. sanguinea (Without locality, *Marloth 7686*, PRE).

Cells with pitted surface (pits 1–1,5 μm diameter), with deeply undulate margin, 200–300 × 30–50 μm (Fig. 2F).

U. modesta (near Premier Mine (2528C), *Young s.n.* sub Tvl. Mus. *32493*, PRE).

Cells with almost smooth surface, rectangular, c. 65 × 20–25 μm (Fig. 3A).

U. modesta (Albany district above Rabbits Wood (3326B), *Jessop 853*, RUH).

Cells not distinguishable, with irregular surface (Fig. 3B).

U. multisetosa (Willow Park, Pretoria (2528C), *Strey 3054*, PRE).

Cells with smooth surface, with undulate margins, 100–130 × 50–60 μm.

U. multisetosa (Duiwelskloof (2330C), *Scheepers 686*, PRE).

Cells with smooth surface, with irregular margins, 150–210 × 40–100 μm (Fig. 3C).

U. marginata (Richtersveld, *Pillans 5780*, BOL).

Cells with smooth surface, with undulate margins, 120–150 × c. 50 μm (Fig. 3D).

Drimia and *Urginea* can be shown, on several bulb and inflorescence characters, to be very closely related. Discussion of the seeds of both is, therefore, treated together. There is considerable variation in cell shape, but the cells are generally clearly recognisable. In one specimen of *U. modesta* they are subrectangular, but in the other specimen of the same species they are probably constricted in the centre although the outline is poorly defined. Several specimens have rather deeply undulate margins (e.g. *U. fragrans*). In a few specimens (e.g. *U. delagoensis*) the boundaries of cells are poorly defined. In surface characters there is also considerable variation from smooth (e.g. *U. pusilla*) to pitted (e.g. *U. delagoensis*). In *U. fragrans* there is a reticulation of minute ridges.

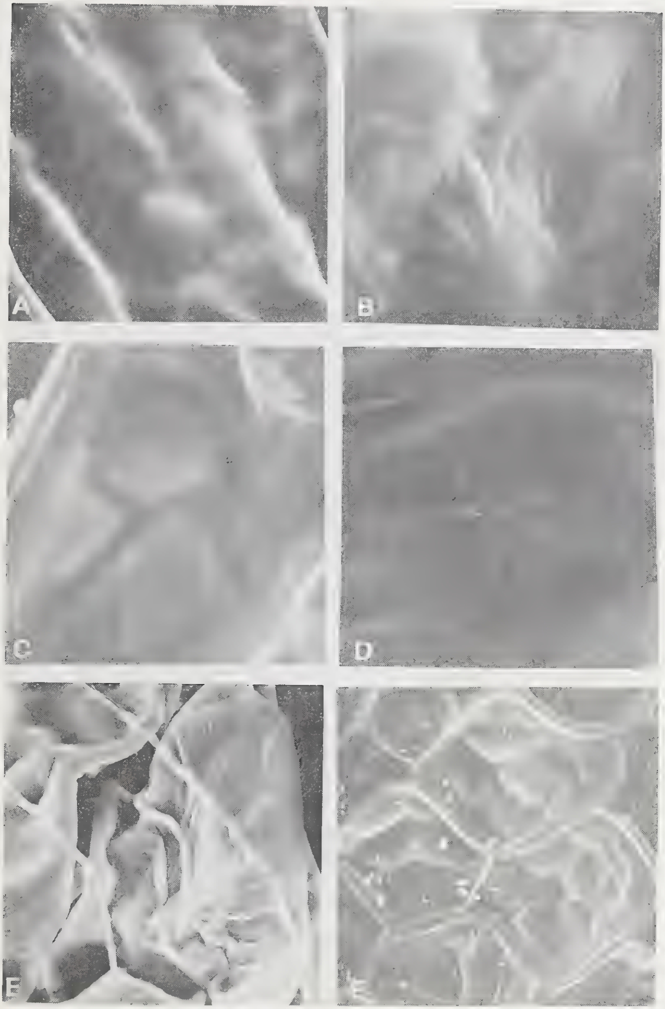

FIG. 3.
Scanning electron microscope photographs of Liliaceae seed surfaces. A. *Urginea modesta* (*Young s.n.*) x 700. B. *Urginea modesta* (*Jessop* 853) x 700. C. *Urginea multisetosa* (*Scheepers* 686) x 700. D. *Urginea marginata* (*Pillans* 5780) x 700. E. *Litanthus pusillus* (*Jacot Guillarmod* 3233) x 700. F. *Rhadamanthus platyphyllus* (*Hall* 3473) x 200.

Because of the variation it is not possible to compare these genera as a whole with other genera. There does not appear to be any correlation with the normal division of this group into two genera in the sense of, for example, Phillips (1951).

Litanthus

L. pusillus (Lesotho, Mamathes (2927B), *Jacot Guillarmod 3233*, RUH).

Cells mostly not distinguishable, with a considerably folded surface, rough with ridges up to 1 μm thick, 5- or 6-angled, c. 20–25 μm diameter (Fig. 3E).

The rather poorly defined cells are somewhat similar to those of one specimen of *Urginea modesta*, but the rugulose surface is unique amongst the samples examined.

Rhadamanthus

R. platyphyllus (Strandfontein, Vredendal (3118C), *Hall 3473*, NBG).

Cells smooth, 4- to 7-angled, isodiametric to oblong, depressed, 80–240 μm diameter. Underlying cells forming shallow convexities in the surface of the superficial cells (Fig. 3F).

R. sp. (Ex hort., Rhodes University).

Cells smooth, 5- or 6-angled, depressed, 70–150 × 50–70 μm. Underlying cells forming shallow convexities in the surface of the superficial cells.

In both specimens examined the cells are exceptionally clearly delimited by prominent marginal ridges. The underlying cells are also distinct. It is possible that the gold palladium may not have been thick enough to prevent a large number of electrons from passing through the surface of the seed. But as this phenomenon was not observed in samples of other genera it is believed to be due to a characteristic in the seed surface.

Dipcadi

D. ciliare (Bushman's River Mouth (3326D), *Noel s.n.* sub RUH *12089*, RUH).

Cells pitted with numerous shallow pits c. 1 μm diameter, 5- or 6-angled, 60–130 × 30–45 μm. Some cells appeared to be abruptly raised above the surrounding cells, but this may be an artefact (Fig. 4A).

D. viride (Burnt Kraal, near Grahamstown (3326B), *Martin s.n.* sub RUH *9271*, RUH).

Cells smooth, 5- to 7-angled, 40–50 μm diameter (Fig. 4B).

In both of the species examined the cells are 5- or 6-angled (rarely 7-angled), not often more than twice as long as broad. The most similar species examined are in the *Urginea-Drimia* group (in which the cells are not as distinctly angled, however), and in *Rhadamanthus* (in which the margins are raised and the underlying cells visible).

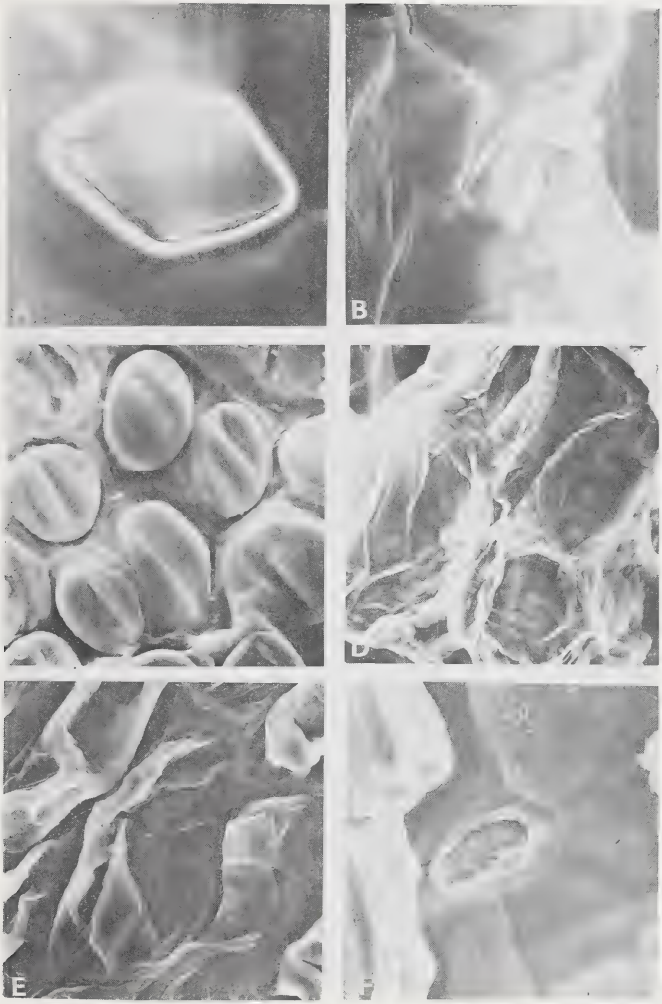

FIG. 4.
Scanning electron microscope photographs of Liliaceae seed surfaces. A. *Dipcadi ciliare* (*Noel s.n.*) x 700. B. *Dipcadi viride* (*Martin s.n.*) x 700. C. *Scilla firmifolia* (Ex hort., Rhodes University) x 700. D. *Scilla nervosa* (*Leendertz s.n.*) x 700. E. *Scilla natalensis* (*Mogg* 2238) x 700. F. *Ledebouria floribunda* (*Van der Merwe* 2240) x 700.

Scilla

S. firmifolia (Ex hort., Rhodes University).

Cells distinctly papillose (the papillae rather flattened with three grooves), 5– or 6–angled, 25–35 μm diameter (Fig. 4C).

S. nervosa (Warmbaths (2428C), *Leendertz s.n.* sub Tvl. Mus. 28064, PRE).

Cells indistinct, probably 5– or 6–angled, 30–40 μm diameter; structures resembling thin-walled papillae present (Fig. 4D).

S. natalensis (Pietermaritzburg (2930C), *Mogg 2238*, PRE).

Cells indistinct, probably 5– or 6–angled, 30–40 μm diameter; structures resembling thin-walled papillae present (Fig. 4E).

Three of the four species of *Scilla* recognised by Jessop (1970) were examined. In both *S. nervosa* and *S. natalensis* there is a wrinkling of the surface which may be caused by the collapse of the convex outer walls. In *S. firmifolia*, however, there are large papillae each with 1–3 (usually 3) furrows. If the appearance of the former two species is caused by the collapse of thin-walled papillae, the differences between them and *S. firmifolia* may not be as great as the first impression of the photographs may suggest. Although the cells of *S. nervosa* and *S. natalensis* are indistinct it is thought likely that all species have 5– or 6–angled cells. These observations give support to the retention of *S. nervosa* in *Scilla* rather than in *Schizocarphus* as proposed by Van der Merwe (1943).

Ledebouria

L. floribunda (Happy Rest, Soutpansberg, N. Tvl., *Van der Merwe 2240*, PRE).

Surface very irregular; the outermost layer (wax-like in appearance) apparently damaged. Cells arranged in regular rows, more or less 4-angled, 15–25 μm diameter (Fig. 4F).

It is not certain that the cell-like patterns are in fact cells as the larger cell-like shapes are subdivided by shallower grooves. There is a close similarity with the *Massonia* group and possibly with *Lachenalia*. The round structure in the photograph is thought to be a result of damage.

Eucomis

E. autumnalis var. *clavata* (Tabamhlope, Estcourt (2929B), *Downing 53A*, PRE).

Shallow depressions over whole surface c. 20–40 μm diameter. Minute, more or less reticulate, ridges c. 0,1 μm wide over both raised and depressed portions, otherwise smooth (Fig. 5A).

The surface shows no evidence of cells and is similar to some members of the *Massonia* group.

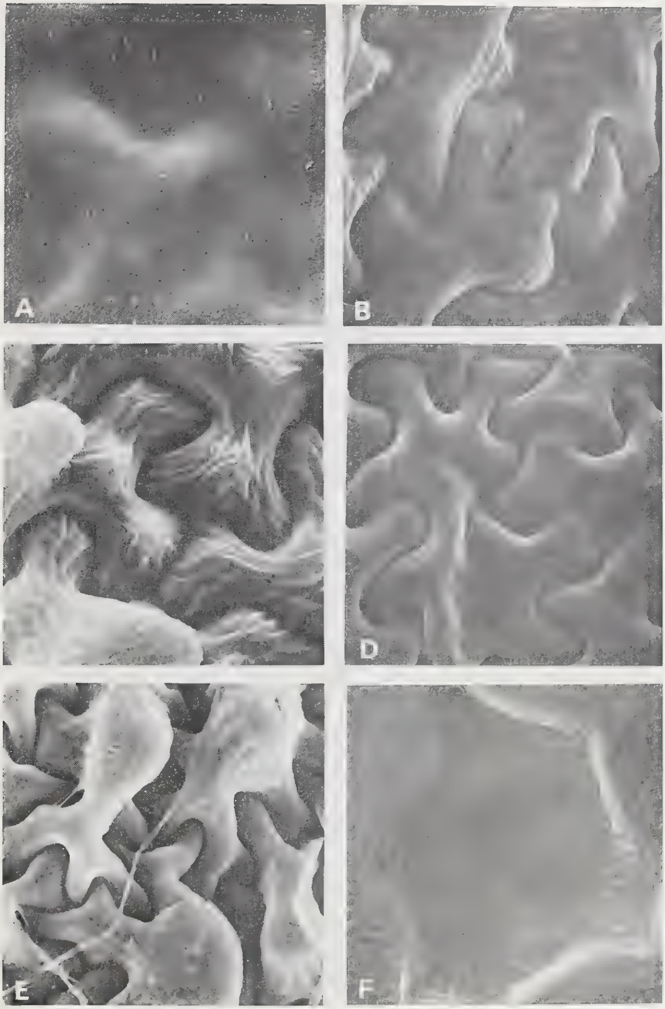

FIG. 5.
Scanning electron microscope photographs of Liliaceae seed surfaces. A. *Eucomis autumnalis* var. *clavata* (*Downing* 53A) x 700. B. *Ornithogalum thyrsoides* (Bought at Houtbay Neck) x 700. C. *Ornithogalum conicum* (*Leipoldt* 4374) x 700. D. *Ornithogalum ceresianum* (*Goatcher s.n.*) x 700. E. *Ornithogalum miniatum* (*Muir* 2988) x 700. F. *Pseudogaltonia clavata* (*Tölken s.n.*) x 700.

Ornithogalum

O. thyrsoides (Table Mountain above Kirstenbosch (3418A), *Bolus 4919*, PRE).

Cells with smooth surface but separated from one another by deep grooves, with undulate margins, 110–150 × c. 50 μm.

O. thyrsoides (Bought at Houtbay Nek, PRE).

Cells with smooth surface but separated from one another by deep grooves, with undulate margins, 110–150 × c. 40 μm (Fig. 5B).

O. conicum (Clanwilliam (3218B), *Leipoldt 4374*, PRE).

Cells papillose (the papillae verrucose), with undulate margins, 90–140 × 30–40 μm (Fig. 5C).

O. ceresianum (Ceres (3319A), *Goatcher s.n.* sub BOL *13726*, PRE).

Cells with smooth surface, with undulate margins, 90–130 × 40 μm (Fig. 5D).

O. maculatum (Sandberg near Clanwilliam (3218B), *Leighton s.n.* sub BOL *2161*, PRE).

Cells with minutely verrucose surface, deeply grooved between the cells, with undulate margins, 65 × 20 μm.

O. miniatum (Near Riversdale (3421A), *Muir 2988*, PRE).

Cells with numerous shallow depressions c. 1,0 μm diameter, with undulate margins, c. 70 × 20 μm. Each cell produced into a papilla up to 70 μm long (Fig. 5E).

O. miniatum (Kommaggas (2917D), without collector sub Stellenbosch University Garden no. *3983*, PRE).

Cells with numerous shallow depressions c. 1,0 μm diameter, with undulate margins, 70–80 × c. 20 μm. Each cell produced into a papilla up to 80 μm long.

The seven specimens examined were all very similar, with deep grooves between the cells and the outer tangential walls strongly convex or produced into papillae. There is a similarity with *Galtonia princeps* and, to a limited extent, with *Albuca* and the *Urginea-Drimia* group, but these genera have flatter cells.

Pseudogaltonia

P. clavata (Sturmveld, Gobabis (2119), *Tölken s.n.*).

Cells with surface reticulately patterned with shallow depressions c. 20 μm diameter, sub-isodiametric, 5- to 7-angled, 65–100 μm diameter (Fig. 5F).

The cell pattern is similar to that in *Scilla* and *Dipcadi*, but the surface reticulation is more similar to that of a few species of the *Urginea-Drimia* group.

Lachenalia

L. monophylla (Storms River (3323D), *Seagrief s.n.* sub RUH *22228*, RUH).

Surface wrinkled, with a pattern of subrectangular cells c. 30–40 × 30 μm (Fig. 6A).

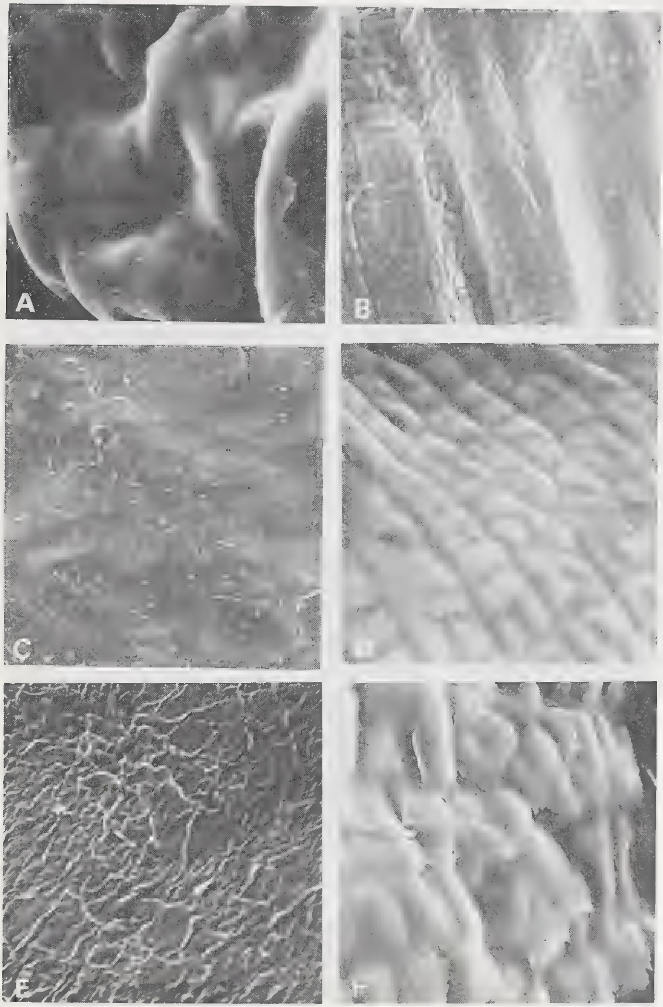

FIG. 6.
Scanning electron microscope photographs of Liliaceae seed surfaces. A. *Lachenalia monophylla* (*Seagrief s.n.*) x 700. B. *Whiteheadia bifolia* (*Hardy* 542) x 200. C. *Neobakeria angustifolia* (*Friedlander s.n.*) x 700. D. *Massonia depressa* (*Marloth* 10367) x 700. E. *Massonia echinata* (*Bayliss BS*/4868) x 3000. F. *Massonia putulata* (*Acocks* 21339) × 700.

The absence of surface details allies this specimen with the *Massonia* group.

Whiteheadia

W. bifolia (Ratelpoort between Springbok and Steinkopf (2917D), *Hardy 542*, PRE).

Surface wrinkled, with rows of more or less 4-angled cells 10–23 μm diameter (Fig. 6B).

Examination of freezing microtome sections confirmed that the cell-like convexities agree in size with the epidermal cells and are, therefore likely to indicate the cell walls.

Neobakeria

N. angustifolia (De Aar (3024C), *Friedlander s.n.*, GRA).

Surface smooth except for cells which are 5- or 6-angled and 20–30 × c. 10 μm. This seed belongs to the *Massonia* group (Fig. 6C).

Massonia

M. depressa (Without locality, *Marloth 10367*, PRE).

Surface smooth except for cells arranged in rows and 7–10 μm diameter (Fig. 6D). Freezing microtome sections confirmed that these patterns do represent cells.

M. echinata (Near Klipplaats Village (3324A), *Bayliss BS/4890*).

Surface coarsely verrucose with ridges down to less than 1 μm diameter. Cells not distinguishable.

M. echinata (Near the Redhouse turnoff (3325D), *Bayliss BS/4868*).

Surface coarsely verrucose with papillae and ridges down to less than 1 μm diameter. Cells not distinguishable (Fig. 6E).

M. pustulata (Locality not recorded, *Acocks 21339*, PRE).

Surface smooth except for more or less square cells c. 10–15 μm diameter (Fig. 6F).

Epidermal cells are either not recognisable or (as in *Whiteheadia*) there are rectangular or triangular cells.

Daubenya

D. aurea (Sutherland (3220A), *Marloth 7106*, PRE).

Surface smooth except for cells which are 4- to 6-angled and 18–23 μm diameter (Fig. 7A).

The cell pattern is similar to that in *Whiteheadia* and in some species of *Massonia*.

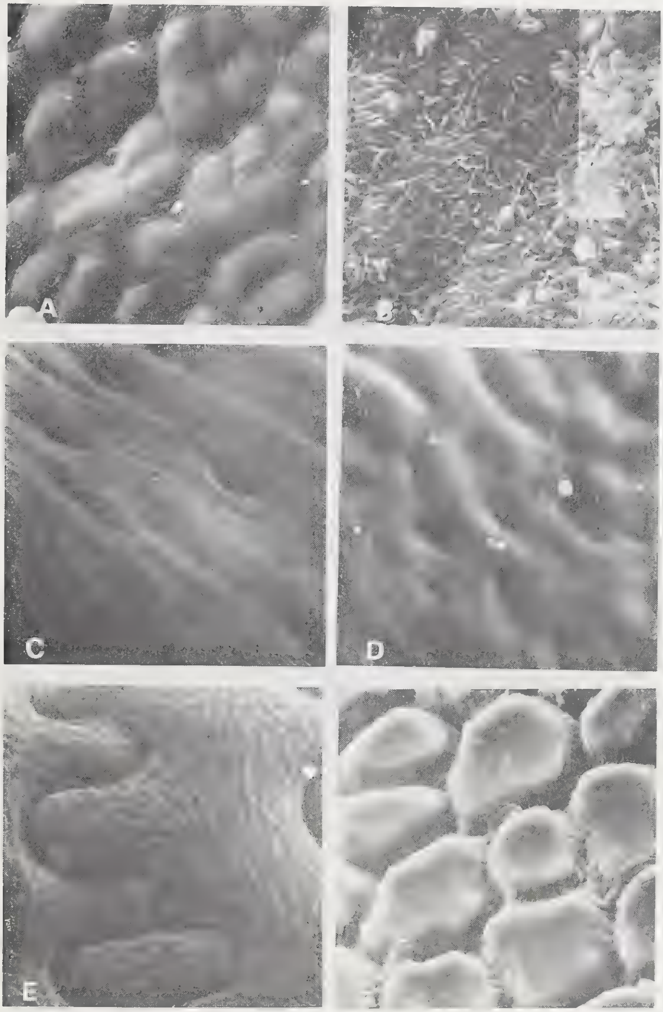

FIG. 7.
Scanning electron microscope photographs of Liliaceae seed surfaces. A. *Daubenya aurea* (*Marloth* 7106) x 700. B. *Androsiphon capense* (*Acocks* 18606) x 700. C. *Polyxena ensifolia* (*Dyer* 99a) x 700. D. *Hyacinthus corymbosus* (NBG 374/64) x 700. E. *Neopatersonia uitenhagensis* (*Long* 135) x 700. F. *Asparagus virgatus* (Ex hort., Rhodes University) x 700.

Androsiphon

A. capense (Farm Plaatberg, S.W. of Calvinia (3119B), *Acocks 18606*, PRE).

Cells 4- to 6-angled, 13–23 μm diameter. Surface naked or densely lepidote; the scales irregular in form and arrangement and up to c.3 μm broad (Fig. 7B).

At low magnifications (×100) the surface appears indistinguishable from other members of the *Massonia* group. However, higher magnifications showed a unique scaly covering of one of the four specimens examined.

Polyxena

P. ensifolia (Oudtshoorn (3322C), *Dyer 99a*, GRA).

Cells not distinguishable. Surface more or less smooth with shallow pits up to c.10 μm diameter (Fig. 7C). There is a close similarity with *Neobakeria angustifolia* and *Hyacinthus corymbosus*.

Hyacinthus

H. corymbosus (Witklip Farm, Vredenburg, without collector sub NBG *374/64*, NBG).

Cells not distinguishable. Surface more or less smooth with shallow pits up to c.10 μm diameter (Fig. 7D).

There is a close similarity with *Neobakeria angustifolia* and *Polyxena ensifolia*.

Neopatersonia

N. uitenhagensis (Bethelsdorp (3325D), *Long 135*, GRA).

Cells pitted (the pits c. 1–1,5 μm diameter), with undulate margins, c. 130–170×60–70 μm (Fig. 7E).

The shape of the cells is similar to that of *Albuca* and to some specimens of the *Urginea-Drimia* group. The pits are reminiscent of the *Urginea-Drimia* group or of *Pseudogaltonia*.

Asparagus

A. virgatus (Ex hort., Rhodes University).

Cells smooth, slightly concave, separated from one another by grooves with almost vertical sides, c. 5–6 μm deep, isodiametric, 5- or 6-angled, 30–40 μm diameter. The raised tubular cells are unlike any others in the material examined (Fig. 7F). *Asparagus* was included for comparison but is not bulbous.

SEED-SURFACE TYPES

Several essentially different types of seed surfaces were observed in the bulbous Liliaceae.

1. The *Massonia* group (*Whiteheadia*, *Lachenalia*, *Ledebouria*, *Massonia*, *Neobakeria*, *Eucomis*, *Daubenya*, *Androsiphon*, *Polyxena* and *Hyacinthus*) possess either no indication of cells or rectangular or triangular shapes (generally about 15 μm diameter) cells.
2. The *Ornithogalum* type (*Ornithogalum*) possesses deeply separated cells with strongly undulate margins.
3. Cells with deeply undulate margins, but flatter outer tangential walls than in *Ornithogalum* (*Albuca*, *Galtonia* and *Neopatersonia*).
4. Angular cells (*Scilla*, *Dipcadi*, *Rhadamanthus* and *Pseudogaltonia*).
5. *Drimia*, *Urginea*, *Litanthus*, *Schizobasis* and *Bowiea* do not fit exactly into any of the above types although certain species of the *Urginea-Drimia* group could be allocated to types 3 or 4. Other species have less deeply undulate outlines than in the previous types or more or less rectangular cells.

Generic Groupings

The Bowieae (*sensu* Hutchinson) deviate further from the norm of bulbous Liliaceae than do any of the other previously proposed groups. Within this tribe there are, however, two very different elements. *Bowiea* and *Schizobasis* have bulbs, no foliage leaves in the mature plant and spurred bracts. *Eriospermum* has a tuber, foliage leaves (usually hysteranthous) and bracts without spurs. *Eriospermum*, in the absence of a bulb, is not discussed further here.

The affinities of *Bowiea* and *Schizobasis* are of interest. They differ from any other South African members of the bulbous Liliaceae in lacking foliage leaves in the mature plant (although they are present in juvenile stages), and in having a branched aerial stem (present also in *Scilla firmifolia*). These two genera resemble several other genera in, what are considered by the present author to be, a number of important characters. These characters are the spurred bracts, absence of starch from the bulb, and loose testa. The genera to which these characters ally them are *Drimia*, *Urginea*, *Rhadamanthus*, *Thuranthos* and *Litanthus*. The flowers and bulbs are similar and the present work on seed surface characters tends to support this conclusion. A basic chromosome number of 10 is probably also a common feature, although further data are required.

Two evolutionary processes must be postulated to explain the relationship between these two groups:

(*a*) reduction in the size of the foliage leaves which are present in the seedlings of *Bowiea* and *Schizobasis* and at all stages of the other genera, but in the former two genera are reduced, to bulb scales only, in the mature plant;
(*b*) development of branches in the inflorescence.

It is suggested that these evolutionary developments, while of undoubted systematic importance, do not justify subdivision of the proposed group including *Bowiea*, *Schizobasis*, *Urginea*, *Drimia*, *Rhadamanthus*, *Thuranthos* and *Litanthus*. So far as is known there are no genera belonging to this group not represented in the South African flora. A revision of *Rhadamanthus* has recently been published (Nordenstam, 1970) and a revision of the remaining genera will be published shortly by the present author.

The only other tribe split off the Scilleae has been the Massonieae (Hutchinson, 1959). Seed surface characters, as shown in this paper, appear to link several genera, including the two placed in the Massonieae (*Massonia* and *Daubenya*). These genera (*Massonia*, *Daubenya*, *Whiteheadia*, *Lachenalia*, *Ledebouria*, *Neobakeria*. *Eucomis*, *Androsiphon*, *Polyxena* and *Hyacinthus*), and *Amphisiphon* and *Drimiopsis* which were not studied, have morphologically similar bulbs, leaves and inflorescences. Most have representatives with leaves marked with various shades of green or red-purple. *Neopatersonia* was regarded by Phillip (1951) as also belonging to this group but seed surface characters appear to provide strong evidence for separating it. Although there are no strong characters for uniting the members of this group, except for the seed surface characters, there are several features uniting various combinations of genera within the group. These are:—

(*a*) *Lachenalia*, *Ledebouria* and *Drimiopsis* appear to have axillary inflorescences (Jessop, 1972). The rest of the genera have not been determined.

(*b*) *Lachenalia pusilla*, which has very slightly zygomorphic flowers, links *Lachenalia* (zygomorphic) with *Polyxena* (actinomorphic). Both genera and *Hyacinthus* (Cape species only) have a tubular membranous bulb scale as well as fleshy scales.

(*c*) The *Eucomis* flower is similar to that of *Massonia*, and *Whiteheadia* forms an intermediate between these genera. The coma occurs in one species of *Neobakeria* as well as in *Eucomis*, although it is not as well developed in the *Neobakeria*. A coma does also occur in a few genera not included in this group—for example in *Muscari* (European and Asian).

(*d*) *Drimiopsis* and *Ledebouria* are separated only on the incurving, subcucullate perianth of the former. In all other respects these two genera are extremely close.

(*e*) *Massonia* forms a natural group with certain other genera as has been pointed out by Phillips (1951). The members of this group are separated from one another on a fairly small number of characters—for example *Daubenya* from *Massonia* on the zygomorphic flower, *Neobakeria* from *Massonia* on the absence of large spathe-like bracts, *Polyxena* from *Neobakeria* on the insertion of the filaments and the membranous bulb scales.

The remaining genera, not placed in the *Urginea-Drimia* group or the *Massonia* group, form a heterogeneous assemblage, with little to link the genera. *Scilla*, *Ornithogalum* and *Dipcadi* occur in South Africa and in Europe and Asia.

Galtonia, *Pseudogaltonia*, *Albuca* and *Neopatersonia* are principally South African but endemic to Africa. *Camassia* occurs in North America only, *Chionodoxa*, *Hyacinthus* (excluding the Cape species belonging to the *Massonia* group), *Muscari* and *Puschkinia* are northern hemisphere in distribution, mainly from Europe and Asia but also North Africa. *Rhodocodon* is endemic to Madagascar. Because of the wide distribution of this group the material has not been available to the present author to examine fully the affinities of these genera.

The following grouping of those genera (other than members of the Aloineae), which have bulbs and which occur in South Africa (or are closely allied to South African genera) is proposed:—

1. Tribe Scilleae *sensu* Hutchinson (1959), emend.
   Bulb containing starch, leaves not spotted or marked, bracts not spurred, seeds with tightly fitting testa and a distinct cellular pattern superficially.
   Scilla, *Ornithogalum*, *Dipcadi*, *Galtonia*, *Pseudogaltonia*, *Albuca*, *Camassia*, *Chionodoxa*, *Rhodocodon*, *Hyacinthus* (northern hemisphere spp), *Muscari*, *Puschkinia* and *Neopatersonia*.
2. Tribe Massonieae *sensu* Hutchinson (1959), emend.
   Bulb containing starch, leaves usually spotted or marked, bracts not spurred seeds with tightly fitting testa and indistinct or no cellular pattern superficially.
   Massonia, *Neobakeria*, *Polyxena*, *Hyacinthus* (Cape spp), *Daubenya*, *Androsiphon*, *Amphisiphon*. *Ledebouria*, *Drimiopsis*, *Lachenalia*, *Veltheimia*, *Eucomis*.
3. Tribe Bowieae *sensu* Hutchinson (1959), emend.
   Bulb not containing starch, leaves not spotted or marked, bracts spurred (or at least the lower), seeds with loosely fitting testa and a distinct cellular pattern superficially.
   Urginea, *Drimia*, *Rhadamanthus*, *Litanthus*, *Thuranthos*, *Schizobasis* and *Bowiea*.

REFERENCES

HUTCHINSON, J., 1959. *The families of flowering plants* **2.** 2nd edition. Oxford: Clarendon Press.

JESSOP, J. P., 1970. Studies in the bulbous Liliaceae: 1. *Scilla*, *Schizocarphus* and *Ledebouria*. *Jl S. Afr. Bot.* **36** (4): 233-266.

JESSOP, J. P., 1972. Studies in the bulbous Liliaceae in South Africa: 2. *Drimiopsis* and *Resnova*. *Jl S. Afr. Bot.* **38** (3): 151–162.

KRAUSE, K., 1930. Liliaceae. In: A. Engler, (ed.) *Die natürlichen Pflanzenfamilien*. 2nd edition. Leipzig: W. Engelmann.

NORDENSTAM, B., 1970. Studies in South African Liliaceae: 3. The genus *Rhadamanthus*. *Bot. Notiser* **123** (1): 155–182.

PHILLIPS, E. P., 1951. The genera of South African flowering plants. 2nd edition. *Mem. bot. Surv. S. Afr.* **25.**

VAN DER MERWE, F. Z., 1943. *Schizocarphus nervosus*. *Flower. Pl. S. Afr.* **23:** t.904.